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# Bilaterial Precambrian Chondrophores from the Ediacara Fauna, South Australia

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ABSTRACT: A second genus of bilaterally symmetrical Chondrophores has been found in the Late Precambrian at Ediacara Range, South Australia. *Chondroplon bilobatum* new genus, new species, is similar to *Ovatoscutum concentricum* Glaessner and Wade in details of the extreme bilaterality that sets them both apart from previously-described Phanerozoic Chondrophores. The new family Chondroplidae is proposed to contain them.

## INTRODUCTION

The uppermost Precambrian Pound Quartzite at Ediacara Range has attracted worldwide attention for the variety of its fauna and their remarkably good state of preservation. It continues to yield occasional new forms as well as additional (and sometimes very informative) specimens of known species. On a collecting trip in August 1968 two specimens were secured of one of the rarest groups, the Hydrozoan order Chondrophorida. These specimens were a new form and a well-preserved fragment of *Ovotoscutum concentricum* Glaessner and Wade (1966), hitherto known only from its holotype. A small specimen was later found at Brachina Gorge in a fossiliferous deposit equivalent to that at Ediacara (Wade, 1970). The new form is strikingly different from *Ovatoscutum* in shape and in details of its structures but nevertheless shows a much closer relationship to it than to any other genus. These differences and resemblances are taxonomically expressed below by describing the new form as *Chondroplon bilobatum*, new genus, new species, and proposing the new family Chondroplidae to include *Chondroplon* and *Ovatoscutum*.

## ACKNOWLEDGMENTS

I am indebted to Mr. I. M. Thomas, Zoology Dept., University of Adelaide, for supplying comparative material of the modern Chondrophores *Velella* and *Porpita*, and for permission to dissect *Velella*. Professor M. F. Glaessner thoroughly criticized the manuscript, to the great benefit of its final form. My collecting trip was supported by an Australian Research Grant to Professor Glaessner.

DEPOSITORY: The material is deposited in the collections of the Geology Dept., University of Adelaide, Nos. F17335a, b, F17336, and F17338.

## STRATIGRAPHIC POSITION

Ever since the discovery of Precambrian fossils at Ediacara Range it has been known that they occurred just below the top of the Pound Quartzite (Sprigg, 1947). They occupy a zone or 'main fossiliferous unit' about 12 m thick which also contains unfossiliferous strata in various positions and places (Goldring and Curnow, 1967; Wade, 1968). This main fossilferous unit outcrops around all but the N. side of a syncline which is elongated N.-S.; there the area where it should outcrop is buried under a broad scree. The oldest fossils known from Ediacara Range (Glaessner and Wade, 1966; Wade, 1968) were those of the pennatulacean *Pteridinium cf. simplex* (Gürich). These came from a train of boulders on a hilltop at the southeast of the syncline. As the massive fine-grained sandstone of which they are composed is very rare in the sequence, and they are strung out parallel to the strike of the underlying beds, they were thought to be almost *in situ* and no more than 18 m below the main fossiliferous unit, though their exact position in the sequence was unknown. Their unfossiliferous and rather intermittent equivalents were since found 7 m below the main fossilferous unit at the S. end of the synclinal outcrop. After tracing this bed over a mile W. and then N. around the syncline, al-

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most to the limit of its outcrop, two further fossils were found, another well-preserved pennatulacean, *Arborea arborea* (Glaessner) and, *in situ,* the large new Chondrophoran float described here.

The second specimen of *O. concentricum* is from the lower bed of the main fossiliferous unit on the NW. side of Gap Creek Fault, opposite Greenwood Cliff. It was not *in situ* but is of characteristic lithology.

Genus **Chondroplon** n.gen.
Type species **Chondroplon bilobatum** n.sp.

DIAGNOSIS: As for type species.

**Chondroplon bilobatum** n.sp.
(Pl. 6, figs. 1-4; Fig. 1)

HOLOTYPE: F17335 a, b, counterparts of a unique specimen.

PRESERVATION: The preserved portions are a negative mould collected *in situ* and the positive mould that fitted into it from above. Owing to differential weathering the specimens partly complement each other's shape. The negative mould shows part of the proximal third of both lobes of a bilobed body (see Pl. 6 fig. 2). The positive mould shows most of the left side and little of the right side (Pl. 6, fig. 1).

The main body of the fossil is inflected by five large, radial folds, with a maximum measurable relief which reaches nearly 1·5 cm on the right side which is the concave side of the now slightly-curved axis. The weathering of the slabs makes interpretation of the five folds difficult. The three on the left side die out before the margin and the more distal rigbt-side fold appears to have done this. The fifth fold is so much tbe largest that it may have extended to the edge of the disc, but tbere is a convergence between the flaking of platy weathering that appeared in the field to parallel the little evidence of bedding, and the surface of the fossil. The proximal (see p. 186) right margin and possibly also the right proximo-lateral margin must have projected into the water for some time after the burial of the remainder of the partly sand-filled float. Its present position indicates the fossil was buried in a generally horizontal position with widely-spaced, upwardly-acute ridges lying radially between the flat earliest chambers and (except for the largest ridge) a considerable distance inside the margin. Perhaps the initial shape was slightly domed, for sharp, radial folds, not symmetrically placed, their more acute angles directed into a chambered body, do not seem explicable as a natural structure. Although the axis is curved and chambers seem to be smaller on the right side than the left at the proximal end (Pl. 6, fig. 1, 2; Fig. 1), it is not possible to tell how much of the proximal right side is lost, or whether, or how much, the convex side of the axis was stretched and the concave side compressed, during burial. The original specimen may have had a symmetrical body throughout growth; preserved portions of the later 2/3 of the chambers are identical. The facts that the large folds in the float reach their maximum on the concave side of the axis, and that the curvature is mainly at the distorted end of the float, support the view that curvature of the axis is fortuitous. The proximal edge is upturned and folded back through 180°, seriously distorting the proximal ends of the earliest chambers. The upward turn of the proximal edge of the float, the curvature of the axis, and the large folds in the float are probably artifacts induced by conditions of burial such as being dragged at by moving water when partly filled and covered by sand. The massive nature of the bed in which it was deposited is quite exceptional in this area. Where broken at the right side, and in several other places, the depositionally upper surface of the float is seen as a mould in the rock. Over much of the area, however, the upper and lower surfaces are separated by a layer of sandstone fill which is cut through by a series of smooth partings that slope proximally from furrows in the upper surface (seen as ridges from the inside) to corresponding structures in the lower surface. This sandstone fill is here described as representing a chambered float with inflated upper and lower surfaces furrowed by depressed sutures. The partings (partitions) between adjacent chamber-fills are moderately to extremely oblique depending on how much the chamber—represented by its fill—has been distorted. In places a reticulate pattern on the positive mould seems to result from the interaction of the two surfaces. This reticulate pattern and most other structures are replicated on the negative mould. Both counterparts have a few features which do not have replicas; these are mainly due to some of the sandstone chamber-fillings having been chipped off the positive mould during natural weathering, thus revealing parts that were previously hidden and removing parts now recorded only on the negative mould. The replication makes it clear that the counterparts are to be regarded as positive and negative counterpart moulds (McAlester, 1962; Wade, 1968). The sloping wedges of sandstone chamber-fills are particularly attenuated near the proximal edge. They record a proximal shift of the lower side relative to the upper side; this may be largely due to the folding back of the proximal end.

DIMENSIONS: The left half of the positive mould is 18 cm long. It lacks only the last few minute distal chambers and the edges of the most proximally projecting chambers. The original length is estimated at about 19 cm. The maximum width from axis to edge is 11·9 cm, so the complete specimen would have been appreciably wider than long if the axis was symmetrically placed. The length along the axis from distal notch to the distorted proximal end is 13 cm; probably 1½ to 2½ cm additional length was involved in the distorted area. The distal notch was about 1·2-1·5 cm deep, suggesting a depth of about 2-3 cm

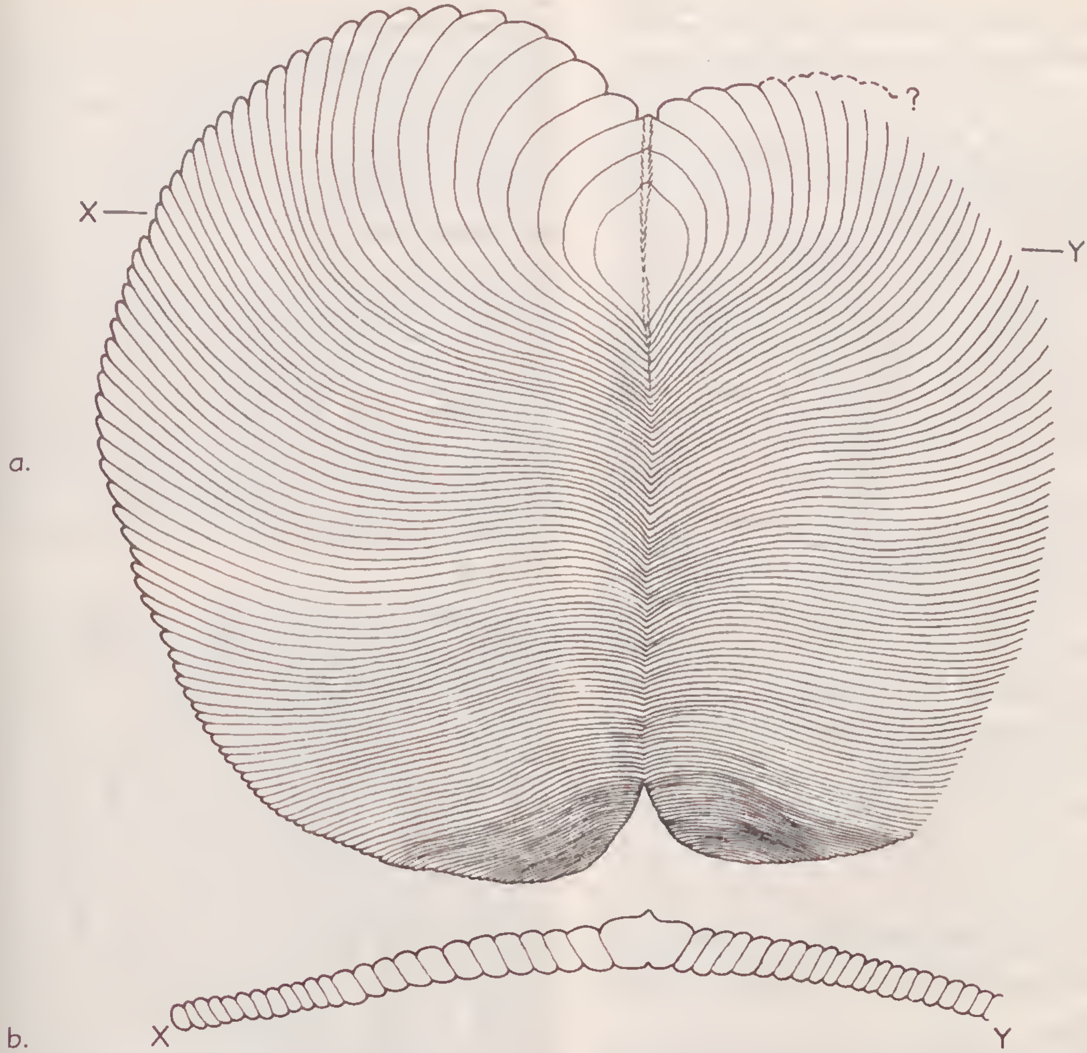


FIG. 1—*Chondroplon bilobatum* n. gen., n. sp., × 0·6. Restored dorsal view, a. and section of float at XY, b. The early chambers appear slightly smaller on the right side than the left but this could be individual variation, as no other asymmetry is indicated by the original material. The ends of all chambers have been restored as simple, rounded lappets like those that frame the proximal notch. The crest on the large initial chamber strengthens towards the proximal notch and was therefore continued across the two annular chambers. Crowding of attenuate late-formed chambers causes darkening of the diagram near the distal notch.

for the proximal notch. The surface is strongly sculptured by over 90 sets of ridges and furrows which indicate chambers and the position of partitions between chambers.

DIAGNOSIS: Large, bilobed float with a narrow, strongly-marked axis (developed as a ventral groove and probably a blunt dorsal keel); proximal notch formed at proximal end of axis early in growth (after third chamber in holotype), distal notch formed at distal end of axis late in growth (after 76th chamber in holotype); initial chamber relatively large, rather elongate, pointed distally (undistorted shape of proximal end unknown, but possibly also tapering); early chambers annular, later chambers progressively less embracing, varying in shape from almost encircling, through crescentic, to slightly sigmoidal half-chambers divided by the proximal notch; chambers higher than broad (where both surfaces visible); individually, chambers narrow toward distal part of axis and broaden away from it, being broadest adjacent to the periphery where they end in rounded lappets; in general, chambers diminish in breadth distally, until very narrow; early chambers increase in length, later length holds constant, and then diminishes; (greatest length of individual chambers reached before widest portion of float in holotype, chambers from about

20th to 40th equally long, greatest width of half float at 43rd chamber); surface strongly ornamented by depressed sutures between inflated chamber surfaces.

DESCRIPTION: The fossil consists of two rounded lobes, each more than semi-circular in outline, united along a narrow *axial furrow* (Pl. 6, fig. 1-3). The *initial chamber* is large, over 1·8 cm wide and 2·5 cm long, though the length is doubtful due to distortion. It was probably originally spindle-shaped, and is situated near one end of the axis. This is here called the *proximal end*, both of the axis and the fossil (Pl. 6, fig. 3). The second and probably the third *chambers* are completely embracing, all later chambers are progressively less embracing, leaving a notch between them at the proximal end; this is the *proximal notch*. As the rate of increase in length of chambers was not as great as would have been needed to maintain forward growth of the chambers, the proximal notch widened rapidly; it reached a maximum at the 8th chamber, later chamber-ends retreated distally around the circumference. Maximum chamber-length was reached about the 20th chamber and held constant to the 40th, thereafter it diminished regularly to the 76th chamber, after which a *distal notch* formed at the *distal end* of the axis, halving the chambers and causing the half-chambers to diminish at both ends, that is, much more rapidly. The complex factors of changing chamber-length are superimposed on fairly constant factors of breadth. All chambers are narrowest adjacent to the distal part of the axis and broaden away from it. Overall, they diminish in breadth from first to last. Near the last they are so narrow that they are not clearly preserved because the grain size of the sediment blots them out, but over 90 and probably about 100 were present. The last few mm of the float were weathered away, removing an unknown number of chambers or incipient chambers.

Wherever the peripheral ends of the chambers are preserved they appear to be rounded lappets. Near the centre of the proximal notch the fossil is contorted and stretched, as this portion of the body is folded upward and backward through 180°. Here chamber-ends appear to have been single lappets for each chamber, though very few sutures can be traced around the folded edge to join those delimiting the chambers seen from below. The periphery is present also on the left side and here the lappets are angled distally and appear double, with the depositionally lower portion folded over distally as a D-shaped lappet (Pl. 6, fig. 4). The doubling is interpreted as a probable preservational feature, p. 187.

The main body of the fossil is dominated by the *lower surface* (that which was downward as buried). A cast from the natural mould shows this surface 'ornamented' by furrowed sutures between the chambers which are smoothly inflated in places but elsewhere, particularly where they are broadest, are flat to slightly concave. The positive mould shows structures at 3 levels (Pl. 6, fig. 3): (1) On the lower surface, appearance as described for the cast from the natural mould. (2) Exposed by chipping, 'concentric' lines formed by the chamber-fillings having been compressed against one another. These fillings grade from narrow prisms (as seen in section on the broken right side) to attenuated flanges of sandstone (Pl. 6, fig. 3a, b). All slope more or less strongly to the proximal end, the partitions and surfaces being almost parallel as the distorted proximal end is approached; in this area the displacement is measurably greater than at 'a' (Pl. 6, fig. 3). Evidently the whole lower surface moved proximally in comparison to the upper surface. (3) The *upper surface* (essentially, an external mould) is exposed 'c', 'd' (Pl. 6, fig. 3). The surface seen at 'c' is a mirror image of any similarly unflattened portion of the lower surface. At 'd' the interior of the first chamber is exposed. In addition to its possible boundaries 'e' and to fortuitous creases it shows a furrow 'f' of the same dimensions as the axial furrow 'g' seen on the lower surface. On the negative mould 'g' ends near a small, oval area at the centre of the initial chamber (Pl. 6, fig. 2).

RECONSTRUCTION: As the positive composite mould has parts of both upper and lower surfaces exposed, and elongate prisms to flattened flanges of sandstone between them, it is legitimate to restore it as a thin-walled, chambered structure (float) which was partly filled by sand prior to burial. The apparent axial groove, 'f', seen on the upper wall from inside the initial chamber is deeper than either the apparent thickness of the wall or any restored thickness for it which can be based upon equivalent structures in modern Chondrophores. It thus seems possible that it represents an axial keel on the supper surface. In other words, the upper surface would be the dorsal surface in comparison with later Chondrophores. The evidence for this keel is not conclusive, however, since 'f' could be a fortuitous fold even though it has been shown as a keel on Fig. 1. It extends across the revealed portion of the initial chamber, diminishing toward its centre where it is hidden by chamber-fill, and proximally is lost to view among the creases at the distorted, upturned, proximal edge. The proximal view of the upturned surfaces of the second and third chambers also shows an axial groove; as this does not seem to have been revealed by the weathering away of the chamber fillings, it seems likely that this is the outside view of the lower surface, and that its axial groove extended across probably two annular chambers, to the apex of the proximal notch. The upper surface at the proximal end is more creased than the lower surface seen on the latex cast of the negative mould. While this could be explained as wholly due to the upper surface being on the inside of the curve, there remains a strong probability that the earliest chambers were not only the broadest but the highest, and that the centre of the float was rather peaked, as restored in Fig. 1b. As the second chamber overlaps the first from the left and right sides (Pl. 6, fig. 3) the restoration Fig. 1b shows some initial slope on the partitions between chambers—but it is not thought likely that even the least-tilted of the partings (Pl. 6, fig. 3) is in the original attitude of a partition. Not enough of the right side of the float is preserved to be certain whether it was bilaterally symmetrical but this is possible even though, on the right, the proximal edges of the first few non-annular chambers are smaller than those on the left. Both sides are greatly distorted. Comparable portions of all the later chambers are identical (Pl. 6, figs. 1, 3).

The minute size of the late chambers (Pl. 6, fig. 1) suggests that simultaneous expansion of numbers of chambers was a growth characteristic, rather than one chamber attaining much of its full size before the next was added. As the later chambers were so small, the float was presumably rather delicate in this area and the distal notch could be considered a post-mortem effect. Against this is the fact that the chambers from the last preserved to the inner end of the notch increase rapidly in length, and probably grew at both ends. The axial line would thus originate as a suture.

The margin is one of the most peculiar structures of the shield. Each chamber appears to end in a pair of flattened lappets, the proximal one folded over and back, and the distal simply folded backward (Pl. 6, fig. 4). These structures are identical in the positive mould and the cast from the negative mould, and provide no unequivocal evidence of whether the appearance of double lappets is original or preservational. As the lappets seen proximally appear to be merely rounded ends to individual chambers, and it is difficult to envisage a changed function (and structure) for lateral lappets when all the float was presumably covered by soft tissue as in modern forms, the possibility of this effect being produced by the conditions of preservation must be considered. That the whole lower surface of the float moved proximally relative to the upper surface is established by the degree and direction of slope of the partings (= partitions) between adjacent chamber-fillings; such a movement would act more strongly on the attached (inner) portion of the protuberant chamber-ends than on their tips, and provides a mechanism that would drag the lower surfaces of all the sand-filled chamber-ends proximally with regard to their upper surfaces, their attached inner ends being the most displaced. This would have the effect of bending the chamber-ends as a whole distally, and tilting them. That such a mechanism acted cannot be validly disputed, but whether it caused the whole of the distal bend of the chamber-ends is questionable. It is conceivable that the mechanism described above produced bending of the chamber-ends enough for the general flattening of the fossil to cause them to fold over, their sharply bent walls pinching and dividing their sand fillings (all that now remains) into the more proximal 'lower lappets' which appear folded over and are angled distally, and the more distal 'upper lappets' which are merely angled distally. It is thus not necessary to assume that the double lappets are an original structure while waiting the proof of further specimens.

Remarks: The possession of notches at either end of the axis distinguishes *C. bilobatum* from any other Chondrophore. Its characteristic of steadily less embracing chambers is also unique. Its axial structure is much more definite than the symmetrically placed axis of *Ovatoscutum*, presumably because of a differing mode of growth. The axial line of *Ovatoscutum* makes no more impression on the chamber surfaces than the 'E.-W.' sulcus of the lateral vascular vessels of *Velella* or *Plectodiscus* Ruedemann (Caster, 1942). The association of this axial line with the notch and the bisymmetrical chamber shape, however, indicates that it is not a pair of lateral canals. This emphasizes the basic bilateral symmetry of *Ovatoscutum* (and *Chondroplon*), while the lack of a raised centre and sail also differentiates it from *Plectodiscus*.

The available evidence for *C. bilobatum* (Pl. 6, figs. 1-3) suggests the action of compression on depressed sutures and smoothly-inflated chamber surfaces as the cause of its ridged ornamentation which is now closely similar to the 'concentric' ornamentation seen on the holotype of *Ovatoscutum concentricum*, Glaessner and Wade. This resemblance is almost certainly superficial, as the new fragmental specimen of *O. concentricum*, much less flattened than the holotype has steep-sided, round-topped ridges marking the position of sutures between chambers which have flat surfaces. Relics of this condition are also seen on the less-flattened portions of the anterior chambers of its holotype. The small individual had very narrow ridges between its flat-topped chambers (Pl. 6, fig. 5). Its axis and other characters are as described for the holotype (Glaessner and Wade, 1966). Sclerotization probably diminished posteriorly, for the definition of chambers ceases in an irregular manner as in the holotype, leaving a wide, posterior notch after about 10 chambers.

To compare *C. bilobatum* with *O. concentricum*: both have a narrow axis, and in both individual chamber-breadth is greatest adjacent to the axis at one end and smallest at the other. The end of the axis where chambers are broadest was designated 'anterior' in the description of *O. concentricum* (Glaessner and Wade, 1966). The term 'proximal' (used here for description of *C. bilobatum* where this end is formed prior to the opposite or distal end) is preferable as the Chondrophores lack an anterior and a posterior definable in terms comparable to general usage in invertebrates; their major structures are radially symmetrical except in those forms that have a sail, and even in these, the sail is the main deviant structure. There is an obvious difference in structure between the two forms in that notches are formed at both ends of the axis in *C. bilobatum* and only at the distal end in *O. concentricum*. The distal notch forms late in growth in *C. bilobatum* and relatively early in *O. concentricum*. In this form the curvature of the chambers from the proximal part of the axis to the distal notch changes from crescentic inwardly, to nearly parabolic toward the outer edge. The new fragment is of a large specimen; though only the outer part of one side is present the possession of a distal notch can be inferred from the parabolic curve of its chambers. The proximal notch of *C. bilobatum* is formed after only two annular chambers and all succeeding chambers are progressively less embracing. The distinction between this character and the proximally complete chambers of *O. concentricum* would not be greatly affected by the discovery of further specimens of *O. bilobatum* with more or less than 2 annular chambers; it depends on a complex interplay of growth factors. While in *C. bilobatum* the breadth and the degree of embracement constantly diminish, the length of individual chambers first increases, then remains constant, and finally diminishes. In contrast, both the breadth and length of chambers increase throughout in *O. concentricum*, though the rate of increase in length may drop off as the shape of chambers tends towards parabolic. It is remarkable that a distal notch is found in both genera when their antithetic growth-form is the basis of one of their greatest differences. The initial chamber is large in *C. bilobatum* and very small in *O. concentricum.*

The order Chondrophorida was described as consisting of two families, the Porpitidae with strictly radial pneumatophores and the Velellidae with less strictly, but still dominantly, radial pneumatophores. The Late Precambrian bilateral forms fit neither of these families and should be classified in a family of their own.

### Order CHONDROPHORIDA

### Family CHONDROPLIDAE nov. fam.

Type genus **Chrondroplon** nov. gen.

DIAGNOSIS: Float bilaterally symmetrical about a narrow axis. Chambers individually broadest toward one end of the axis (proximal end) and narrowest adjacent to the opposite (distal) end. With a distal notch dividing the later chambers axially, with or without a proximal notch. Initial chambers large or small, later chambers decreasing or increasing in breadth and length.

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## EXPLANATION OF PLATE 6

(All photos unretouched. The proximal ends of all specimens are to the right except in fig. 2.)

FIGS. 1-3—*Chondroplon bilobatum* nov. gen., nov. sp. F1735a, b. 1a) ×½, the positive mould of the float, 1b) ×1·95, the margin between the pointers on 1a. 2) ×1·4, the negative mould. 3) ×1·4, the proximal end of the positive mould; a, chamber-filling exposed between lower surface and upper surface, b, flattened flanges of sandstone representing chamber-fillings; c, upper surface of float chambers; d, upper surface of initial chamber; e, suture around initial chamber; f, possible axial structure of upper surface of initial chamber; g, axial structure of lower surface.

FIGS. 4, 5—*Ovatoscutum concentricum* Glaessner and Wade, F17336, F17338, respectively. 4) ×1, fragment of external mould with depressions representing sutural ridges, natural edge at top. 5) ×1·25, complete small specimen from Brachina Gorge (latex cast).